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Nederlandse samenvatting

De ruimtelijke- en gemeenschapscontext van ecologische specialisatie

Onze wereld is ontzettend heterogeen; van open landschappen tot gesloten bossen, van laagland tot hoogland en van droge vlaktes tot moerassen. Soorten passen zich aan verschillende omstandigheden aan en vertoeven het best onder hun specifieke condities. Denk bijvoorbeeld aan bergduivels (Australische hagedissen) die water verzamelen met hun schubbigheid om de droogte te overleven of aan lama's die gemakkelijker zuurstof kunnen opnemen hoog in de bergen waar ze leven. Het is schitterend om deze aanpassingen te zien, maar toch is het nodig dat soorten ook wat flexibel zijn, aangezien de wereld zowel in tijd als in ruimte vrij dynamisch is. Een boom kan omvallen en een heel nieuwe leefruimte creëren, overvloedige regenval kan het landschap aanpassen, maar ook menselijke invloeden zoals ontbossing en eutrofiëring brengen grote veranderingen met zich mee.

Verschillende landen hebben vorige zomer hun hitte records verbroken. Helaas is dit niet zomaar een eenmalig gegeven, maar een duidelijk signaal van klimaatverandering. De mens bouwt hiervoor onder andere airconditionings, maar kan zich ook gedragsmatig aanpassen of de veranderingen proberen te verdragen. Andere soorten gaan hetzelfde proberen te doen. Als ze dit niet kunnen, betekent dit voor hen het einde. Soorten kunnen zich daarnaast ook genetisch aanpassen aan veranderende omstandigheden al gebeurt dit doorgaans over meerdere generaties. Deze aanpassingen aan wijzigende condities is de rode draad doorheen mijn thesis. Vele soorten worden bedreigd door de klimaatverandering en we kunnen de klok helaas niet volledig terugdraaien. Wat we wel kunnen is proberen te achterhalen welke factoren adaptatie kunnen helpen. Begrijpen onder welke omstandigheden adaptatie waarschijnlijker is, kan helpen voor conservatiedoeleinden en bij het maken van betere voorspellingen.

Soms moeten soorten veranderen van voedsel als hun normale voedselbron bijvoorbeeld sterk afneemt, als andere soorten die hetzelfde voedsel nuttigen plots toenemen in aantal of als soorten van gebied moeten veranderen door gewijzigde biotische of abiotische omstandigheden. Vaak treden er daarvoor genetische veranderingen op of eventueel veranderingen in de darmflora van het organisme. Bovendien zijn er heel wat factoren die een invloed kunnen hebben op de aanpassingen, zoals bijvoorbeeld interacties met andere soorten.

Door middel van experimenten met een geleepotig modelorganisme, de bonenspintmijt of *Tetranychus urticae*, hebben we onderzocht hoe verschillen in ruimtelijke- of gemeenschapscontext adaptatie aan een nieuwe voedselbron kunnen beïnvloeden. De ruimtelijke context in dit onderzoek kan zowel duiden op een eerder homogene of heterogene omgeving, alsook op verschillen in dispersie. De onderzochte populatie bonenspintmijten kwam aanvankelijk enkel voor in een homogene omgeving, de initiële voedselbron van deze soort was immers enkel de

bonenplant. In het onderzoek werden de onderzochte bonenspintmijten in een nieuwe homogene of heterogene omgeving (meerdere plantensoorten samen) geplaatst. De populatie kreeg hiertoe nieuwe plantensoorten zoals komkommer-, tomaten- en paprikaplanten ter beschikking, waaraan de bonenspintmijten zich al dan niet konden aanpassen. Dispersie duidt op het aantal bonenspintmijten dat per week van de oorspronkelijke populatie (op bonenplanten) werd overgezet naar de nieuwe plantensoort. Dit is onderdeel van de ruimtelijke context, omdat het een idee geeft over de afstand tussen de populaties: hoe meer mijten overgezet worden, hoe kleiner de afstand tussen de populaties. Met de gemeenschapscontext bedoelen we de aanwezigheid van een andere soort tijdens de adaptatie (interspecifieke competitie) of de invloed van het aanwezige microbiom (de micro-organismen die in de spintmijten leven en er mogelijk helpen bij de vertering en detoxificatie van voedsel).

In het eerste hoofdstuk beschrijven we het onderzoek naar de invloed van dispersie en competitie op de aanpassing van de bonenspintmijt aan een nieuwe voedselbron, de tomatenplant. We ontdekten dat het wekelijks overzetten van grote aantallen spintmijten van de oorspronkelijke bonenplant nefast was voor de adaptatie aan tomaat. Dit kon vooral verklaard worden door een 'genetic load', hiermee wordt bedoeld dat er te veel onaangepaste allelen (varianten van genen) de aanpassing aan de nieuwe condities gaan tegenwerken. Verder vonden we dat de toevoeging van een andere soort die al aangepast was aan de nieuwe plantensoort (de tomatenspintmijt of *T. evansi*) dit nadelige effect tegenging. Deze andere soort creëerde namelijk een moeilijker omgeving en een grotere sterfte in de populatie bonenspintmijten die adaptatie onderging. Als compensatie was een groter aantal spintmijten per week vereist. Dit grotere aantal kon helpen bij het aanvullen van de populatie en vergrootte de kans op voordelige allelen voor adaptatie. We konden hiermee aantonen dat het noodzakelijk is om zowel de gemeenschaps- als de ruimtelijke context te combineren om een goed inzicht te krijgen in adaptatie.

Tijdens dit experiment werden zowel de veranderingen in prestatie (aantal gelegde eitjes en levensduur; ook wel evolutionaire dynamieken genoemd) als de populatiegroei (of ecologische dynamieken) opgevolgd. Hetzelfde werd gedaan in een ander experiment dat geen onderdeel is van deze thesis (Alzate, Etienne & Bonte, 2019). Beide experimenten gaven ons de mogelijkheid om met behulp van een wiskundig model te onderzoeken hoe evolutionaire adaptatie de draagkracht en groeisnelheid van een populatie kan beïnvloeden (hoofdstuk 2). We konden aantonen dat de draagkracht van de populatie afnam naarmate de populatie beter aangepast was aan de nieuwe omgeving, daarnaast vonden we een toename in de groeisnelheid. Wellicht is dit omdat individuen die beter aangepast waren meer voedsel opnamen, zodat er minder voedsel beschikbaar was voor de overige individuen van de populatie. De extra verworven energie door de hogere voedselinname kon geïnvesteerd worden in een grotere populatiegroei. Dit onderzoek is een mooi voorbeeld van hoe evolutie een effect kan hebben op ecologische dynamieken.

Soms gaan experimenten niet helemaal zoals je het zou willen, maar leiden ze het desalniettemin tot interessante resultaten, zoals in het derde hoofdstuk. Hier wordt het onderzoek beschreven dat wilde nagaan wat de invloed was van een andere mijtensort op adaptatie, maar deze keer een soort die nog niet aangepast was. Onze gekozen competitor, *T. ludeni* of rode spintmijt, stierf helaas uit in ons experiment en wordt daarom in onze studie een geest genoemd. Dit gaf ons de mogelijkheid om te onderzoeken wat de invloed was van initiële selectiedrukken zoals geestcompetitie op adaptatie aan een nieuwe omgeving. Bij sommige populaties bonenspintmijten slaagde de rode spintmijt er initieel wel in om een hogere densiteit te halen. Deze populaties presteerden na 25 generaties nog steeds beter op vlak van fecunditeit dan andere populaties bonenspintmijten. We konden hiermee aantonen dat initiële competitie van een onsuccesvolle soort een langdurig effect kan hebben op adaptatie van een andere soort.

Het vierde hoofdstuk behandelt het onderzoek van opnieuw een combinatie van een ruimtelijke en een gemeenschapscontext, meer specifiek een homogene of heterogene omgeving en competitie. We gebruikten een vrij gemakkelijke voedselbron, komkommer, en de meer uitdagende paprikaplant (door zijn toxische substanties en glandulaire trichomen). De rode spintmijt stierf snel uit en leverde geen nieuwe inzichten op, de variatie in plantensoorten daarentegen was intrigerend. We konden aantonen dat een eerder heterogene omgeving adaptatie aan moeilijke condities kan vergemakkelijken door als het ware een soort evolutionaire stapsteen aan te bieden. Dit betekent dat er voldoende individuen in leven kunnen blijven op de gemakkelijkere voedselbron en op deze manier een populatie in stand houdt die gunstige allelen kan hebben voor aanpassing aan de uitdagende voedselbron. Deze adaptatie was echter kortstondig. Naarmate de populatie op de gemakkelijkere voedselbron uitbreidde, kwamen meer en meer onaangepaste individuen op de paprikaplant terecht die de adaptatie aan paprika teniet deden ('genetic load', zoals beschreven in het eerste hoofdstuk). Adaptatie aan moeilijkere condities kan dus gemakkelijker optreden in heterogene omgevingen, maar is sterk afhankelijk van hoe en hoeveel individuen doorheen het landschap bewegen.

Hierboven werd al vermeld dat het microbiom kan helpen bij het verteren en ontgiften van voedsel, wat het erg waardevol maakt. Hierdoor kunnen deze bacteriën hun gastheer helpen om zich aan te passen aan veranderende omstandigheden. In het vijfde hoofdstuk bespreken we het verdere onderzoek hiernaar met behulp van een evolutionair experiment, door bonenspintmijten zich te laten aanpassen aan twee nieuwe voedselbronnen, nl. komkommerplanten en tomatenplanten. Zowel het microbiom als de fecunditeit en levensduur op de verschillende plantensoorten werden hierbij opgevolgd. We konden aantonen dat het microbiom slechts gedeeltelijk verklaard kan worden door de afkomst en voedselbron van zijn gastheer, maar dus mogelijk voor een groot deel door ongekende factoren wordt beïnvloed. Daarnaast vonden we een correlatie tussen fecunditeit en levensduur op de nieuwe voedselbronnen en het microbiom op deze plantensoorten. Dit toont aan dat de

micro-organismen niet vergeten mogen worden bij onderzoek naar aanpassingsvermogen van soorten.

Geïntrigeerd door de inzichten van het microbioom uit een experimentele omgeving, wouden we dit graag ook onderzoeken in een natuurlijke setting. Hiervoor hebben we veldwerk verricht op microlandslakken op kalksteenheuvels in Maleisisch Borneo. Het doel van dit onderzoek was om interacties te onderzoeken tussen gemeenschappen van slakken, hun dieet en hun microbioom. Onze resultaten toonden aan dat er nauwelijks een correlatie was tussen de slakkengemeenschap en hun dieet, maar dat het microbioom positief gecorreleerd was aan beide. Dit betekent dus dat slakken die leven in een gemeenschap bestaande uit veel verschillende slakkensoorten doorgaans een rijker microbioom hebben, maar ook dat een rijk microbioom gecorreleerd is aan een meer gevarieerd dieet. Daarnaast merkten we dat omgevingsfactoren zoals de grootte van het gebied, de aanwezigheid van grotten en vooral menselijke activiteit een invloed hadden op de slakkengemeenschap, hun dieet en hun microbioom.

Samengevat, adaptatie is een heel complex proces en wordt voor een groot deel beïnvloed door de ruimtelijke- en gemeenschapscontext. In deze thesis hebben we geprobeerd om het proces verder te ontrafelen. Hoewel we in staat waren om meer inzicht te geven in de invloed van dispersie, competitie en het microbioom, is dit slechts de tip van de ijsberg en is vervolgonderzoek aan de orde.

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- Zuk, M. & Travisano, M. 2018. Models on the Runway: How Do We Make Replicas of the World?*. *Am. Nat.* **192**: 1–9.

Curriculum vitae

Education

2014 – 2019

PhD student

Institution

Joint PhD in Evolutionary Biology
Ghent University (UGent, Department of Biology,
Terrestrial Ecology – TERECE)
University of Groningen (RUG, GELIFES, Theoretical
Research in Evolutionary Life Sciences – TRÉS)



2009 – 2014

MSc student

Dissertation

Erasmus

Master in Biology, major in Ecology and Evolution (summa cum laude),
Ghent University

Evolution of ecological specialisation under competition (supervision:
Prof. Dr. Dries Bonte)

Boreal Biota and Ecology Program (University of Helsinki, UH)

BSc student

Dissertation

Bachelor in Biology (cum laude), Ghent University

Groepseffecten bij *Tetranychus urticae* ('group effects within
Tetranychus urticae') (supervision: Prof. Dr. Dries Bonte)

Internships

CRC, KMDA, Antwerp: Helping with ongoing research, such as sexing of
birds and paternity analysis, helping with finalizing genetic diet analysis
by the investigation of manure samples (tutor: Vanya Prévot)

Planckendael, Mechelen: Behavioural observations of bonobos in (tutor:
Evelien De Groot)

Bird Ecology Unit (UH), Helsinki: Census of small mammals (tutor: Diego
Pavon Jordan)

TEREC (UGent): Helping in adaptation experiment study (tutor: Adriana
Alzate Vallejo), monitoring populations and assessing life history traits
(tutor: Annelies De Roissart),

ArcGIS work for insect research on chalk grasslands (tutor: Toos van
Noordwijk)

Teaching Experience

Daily supervisor

2014 – 2019

MSc dissertation (RUG and UGent): supervision of five MSc students

Community Ecology Research course (RUG): supervision of 14 BSc
students

Field Biological Research course (UGent): supervision of 11 BSc students

BSc internship (RUG): supervision of a BSc student from the Indian
Institute of Technology

Teaching assistant

2014 – 2016

Ecology (UGent)

Population Ecology (UGent)

Funding and Awards

- | | |
|------|---|
| 2017 | Leopold III grant for field work in Sabah, Malaysian Borneo |
| 2014 | Special Research Fund (BOF, UGent) for PhD funding |
| | Ubbo Emmius sandwich program (RUG) for PhD funding |
| | Price Pierre Verkerk for best MSc thesis in Biology (UGent) |

Publications

- Bisschop, K.**, Mortier, F., Etienne, R. S., Bonte, D. (2019) Transient local adaptation and source-sink dynamics in experimental populations experiencing spatially heterogeneous environments, *Proc. R. Soc. B*, 286: 20190738
- Hendriks, K. P., **Bisschop, K.**, Kavanagh, J. C., Kortenbosch, H. H., Larue, A. E. A., Richter Mendoza F. J., Schilthuizen, M., Etienne, R. S. (2019) Fieldwork to sample microsnails for diet and microbiome studies along the Kinabatangan river, Sabah, Malaysian Borneo, *The Malacologist*, 72: 33-38
- Alzate, A.*, **Bisschop, K.***, Etienne, R. S., Bonte, D. (2017) Interspecific competition counteracts negative effects of dispersal on adaptation of an arthropod herbivore to a new host, *Journal of Evolutionary Biology*, 30(11), 1966-1977
- Bisschop, K.**, Mortier, F., Bonte, D., Etienne, R. (under review) Performance in a novel environment subject to ghost competition, *PeerJ*
- Bisschop, K.***, Kortenbosch, H. H.*, J. B. van Eldijk, T. J. B., Mallon, C. A., Salles, J. F., Bonte, D., Etienne, R. S. (under review), Microbiome heritability and its role in adaptation of hosts to novel resources, *PNAS*
- Hendriks, K. P.*, **Bisschop, K.***, Kortenbosch, H. H., Kavanagh, J. C., Larue, A. E. A., Phung, C.-C., Bonte, D., Duijm, E. J., Salles, J. F., Pigot, A. L., Richter Mendoza, F. J., Schilthuizen, M., Speksnijder, A. G. C. L., Etienne, R. S. (under review) Microbiome and environment explain the absence of correlations between consumers and their diet in Bornean microsnails, *Ecology*
- Goldenberg, J., D'Alba, L., **Bisschop, K.**, Vanthournout, B., Shawkey, M. D. (under review) Keep it cool: Ventral color evolution in response to substrate heat capacity in ectotherms, *PNAS*
- van Eldijk, T., **Bisschop, K.**, Etienne, R. S. (submitted) Uniting community ecology and evolutionary rescue: Community-Wide Rescue, *Frontiers in Ecology and Evolution*

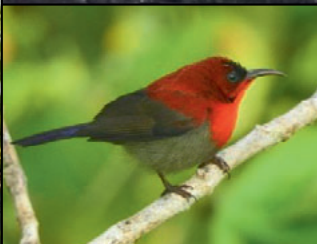
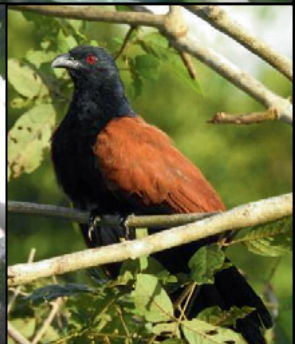
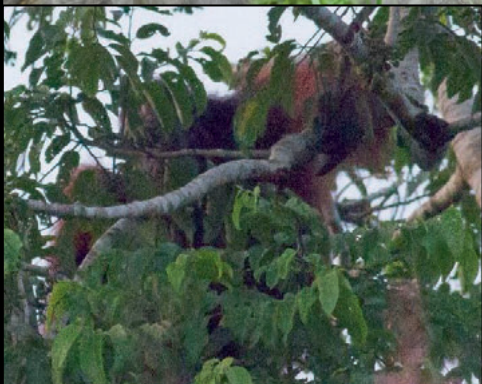
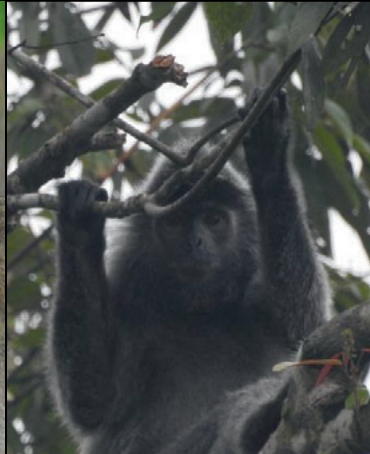
* Joint first author

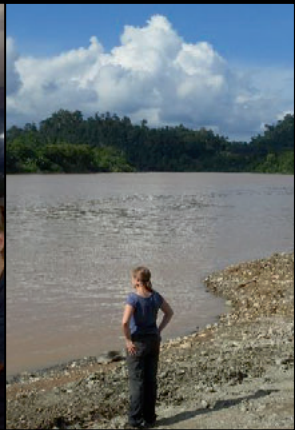
Conferences

- | | |
|------|--|
| 2018 | NAEM , Lunteren, The Netherlands (session convener) |
| 2017 | NAEM , Lunteren, The Netherlands (oral presentation: Unravelling processes behind local adaptation: experimental evolution) |
| | ESEB , Groningen, The Netherlands (oral presentation: Competition and spatial heterogeneity shape eco-evolutionary dynamics of ecological specialisation) |
| 2014 | BES-SFE , Lille, France (oral presentation: Evolution of ecological specialization under competition) |

Additional training

- | | |
|-------------|---|
| 2013 – 2019 | Genetic Modified Organisms (RUG) |
| | Principles of Ecological Genomics (SENSE, Wageningen) |
| | Advanced Biostatistics (UGent, C003345) |
| | Survival Analysis in R (UGent) |
| | Advanced Academic English: Conference Skills – Academic Posters and English Proficiency for Presentations (UGent, Doctoral Schools) |







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